STUDIES IN NORTH AMERICAN PERONOSPORALES—V.

A REVIEW OF THE GENUS PHYTOPHTHORA[1]

Guy West Wilson

(With Plate 119, Containing 5 Figures)

Within recent years our knowledge of this genus has been materially augmented by the appearance of a number of important papers. While it is not the present purpose to present a formal review of all these contributions, it seems worth while to make a general survey of the work which has been accomplished to see what advances have been made in our knowledge of this economically very important genus, as well as to take stock, to use a commercial term, with a view of learning what future lines of investigation promise most valuable results. Perhaps nothing has given greater incentive to the study of this genus or made the progress more rapid than the discovery that these fungi could be grown in pure culture. The first contribution to this subject was by Hecke (1898) who grew *P. infestans* on liquid media such as decoctions of plums, tomatoes, cherries, and potato leaves, but was unable to secure a growth on solid media. Later Clinton (1906) discovered that species of this genus could be grown on solid media other than vegetable plugs. Further discussion of this subject, however, is reserved for a later page. In order to best accomplish our object the various species will be taken up separately, reserving general subjects for the later part of the paper.

1. Phytophthora parasitica Dastur

The most destructive of the few really serious diseases of the castor bean in India is due to this fungus which has been studied in great detail at Pusa (Dastur, 1913). Seedlings are attacked,

[1] Previous papers of this series have appeared in the Bulletin of the Torrey Botanical Club as follows: I. 34: 68–84; II. 34: 387–416; III. 35: 361–365; IV. 35: 543–554. 1907–'08.

causing them to "damp off," while on older plants the leaves suffer most. These are marked with concentrically ringed brown spots. The conidiophores, as is usual in this genus, may emerge either through the stomata or by rupturing the epidermis. The mycelium is both intercellular and intracellular, and often causing a blackening of the vascular bundles. The hyphae are at first quite slender, becoming thicker with age, so that they measure 3–9 μ in diameter. The haustoria are not numerous nor are they differentiated in appearance from young branches. The conidiophores are long and unbranched, usually 100–300 μ tall, but ranging 35–500 μ. The conidia are pyriform, distinctly papillate, 16–60 $\times$ 10–45 μ, and producing from 5 to 45 zoöspores. Intercalary conidia are also found in the cultures which resemble to a considerable extent similar bodies in *Pythium,* but germinating as do the typical conidia. "Varying temperature, alternate light and darkness and moisture are essential factors in the formation" of both conidia and zoöspores. In nature the fungus has been observed to produce conidia sparingly within the tissues of the host, a habit not observed in other species of the genus except *P. infestans.*

Conidial germination, according to the illustrations published, may be either of the typical *Phytophthora* type where each zoöspore escapes separately, or of the *Pythium* type where the entire mass of zoöspores escapes in a vescicle and are later liberated by its rupture. The zoöspores are not different from those of other members of the genus. Chlamydospores are also found in cultures.

The oöspores of this species are formed in the same manner as that described by Pethybridge for *P. erythroseptica.* Indeed the details of sexual reproduction were worked out on these two species simultaneously and independently by Dastur and Pethybridge, each arriving at the same conclusions, although priority of publication made the announcement of Pethybridge precede that of Dastur by several weeks. The most interesting point brought out by Dastur and not by Pethybridge is that the gametes may sometimes arise from the same "stalk" instead of from different ones. When they are on the same hypha the oögonium arises as an ingrowing cell at the base of the antheridium. The

antheridium has reached its full size, or almost so, before the oögonium appears. At the time of the maturity of the oögonium the protoplasm assumes the form of an oöspore and withdraws a little from the thin-walled oögonium, which at the same time becomes thicker walled, and develops a yellowish color. The oögonium measures 18–27 μ in diameter and the oöspores are 15–20 μ, with a thick, smooth, hyaline epispore.

A very interesting portion of the paper is that which deals with the chemical composition of the cell walls, which appears to be the only published account of such studies on a species of *Phytophthora*. It has been stated by previous writers that the cell-walls of the Peronosporales are composed of cellulose only in part, a substance designated callose being present and under certain conditions entirely replacing the cellulose. The tests failed entirely to show the presence of callose in the cell-walls either of the hyphae or the conidia of *P. parasitica*. The only exception to the pure cellulose reaction of the membranes being in the oögonium and oöspore where the inner walls are of a modified cellulose, while the outer walls appear to be of some pectic substance.

The pathogenic nature of the fungus was established by ample experiments. Observations were made which proved conclusively that healthy seedlings planted in the soil in which infected plants had grown within a few weeks past were attacked by the fungus. This is the first time that a species of *Phytophthora* has been positively shown to be able to live in the soil for even a short time although some of them have been strongly suspected of this habit.

Extensive cross-inoculation work with numerous hosts was carried out. Negative results were obtained on cacao, *Cereus, Colocasia, Cleome, Jasminum, Lepidium, Opuntia, Panax, Phaseolus,* and tobacco. Slight or indecisive infections were produced on Areca nuts and lilac. The following were well infected and frequently killed, *Clarkia, Fagopyrum, Gilia, Oenothera, Salpiglossis, Schizanthus, Solanum Melongena, S. Lycopersicum* and *S. tuberosum*. In a field where sesame was grown following castor beans the previous year the stray castor seedlings were attacked by the fungus and later a species of *Phytophthora* indis-

tinguishable from that of the castor bean attacked the sesame seedlings. Reciprocal inoculations proved the two fungi to be identical.

This very interesting fungus is certainly a species of *Phytophthora,* yet its conidial germination, the formation of globose, intercalary conidia, and its ability to live for a time in the soil all point to close relationship to *Pythium.*

2. PHYTOPHTHORA COLOCASIAE Racib.

This species was first described from Java on *Colocasia esculenta* (*C. antiquorum* Schott.) where it is widespread, but not considered of great economic importance. It has since been found in Formosa and over a wide range of teritory in India, where it causes sufficient damage to attract the attention of the workers at Pusa. The results of the studies of Butler and Kulkarni (1913) are highly suggestive of the possible extension of our knowledge of other species of the genus.

On account of the falling of the conidia with a portion of the conidiophore attached after the manner of the pedicel cell of *Basidiophora* and *Kawakamia* the species was transferred by Sawada (1911) to the later genus as *K. Colocasiae.* The fungus is certainly a *Phytophthora,* while *Kawakamia* is more closely related to *Basidiophora.*

Originally described as a leaf parasite, the investigations of Butler and Kulkarni show its activities to be much more widely extended. Not only are the leaf-blades and petioles, and even the inflorescence attacked, but "the parasite commonly reaches the corm and sets up a dry rot during storage," while badly infected plants may even fail to develop corms. This activity is quite suggestive of the tuber-rotting of the potato by *P. infestans.* In this connection it might be remarked that it is not at all impossible that the tuber-rot of *Colocasia* in which was ascribed by Massee to the activities of his *Peronospora trichomata* was in reality due to the attacks of *Phytophthora.*

Detailed studies were made of the fungus both on the host and in pure cultures. The hyphae are quite large (4–9 μ in diameter), with numerous simple, filamentose haustoria. On the aerial parts of the host the fungus is strictly intercellular, except for the

epidermal cells, while in the corm it becomes intracellular, entering both the storage cells and the vascular bundles. The short conidiophores emerge from the stomata. While they are usually simple and bear a single conidium, a second one may be borne in the typical cymose manner of *Phytophthora*. The conidia are quite large ($18–26 \times 30–60\ \mu$ or larger), somewhat pyriform, and more variable both in size and form than in most species of the genus. There is a broad blunt apical papilla.

When mature the conidium "contains a single vacuole of variable size. This is at first irregular and changes shape with the slow movements of the intersporangial protoplasm; then it becomes spherical and ultimately disappears suddenly. The protoplasm itself is at first coarsely granular and after the discharge of the vacuole it is almost homogeneous. About five minutes after the vacuole disappears, the first cleavage lines of the spore-origins become visible and the protoplasm contracts slightly so as to leave a clear space just inside the wall. Soon after, discharge occurs, in the manner so often described for *Phytophthora*, the spores being fully demarcated and provided with cilia before they emerge to the outside." "The zoöspores are more or less bean-shaped, one of the longer sides being convex and the other concave or plane. Each contains a small pulsating vacuole and two cilia arise near together from the concave or plane side, one projecting in front and the other behind while swimming. After swimming for some time they come to rest, round off, lose the cilia and become surrounded by a cellulose wall" (pp. 239–241). A cool temperature facilitates the discharge of the zoöspores. The production of conidia does not appear to be in any way affected by light.

On culture media chlamydospores are common. They vary in size from the diameter of the hypha to $30\ \mu$, and are quite distinct in appearance from the oöspores. As these also occur in *P. Faberi* and *P. parasitica* "it is not impossible that the bodies described as parthenogenic oöspores in several species are really chlamydospores."

Oöspores were produced in various cultures. They are of the same type as is described for *P. erythroseptica* and *P. parasitica*. The oögonia measure $24–35\ \mu$ and the oöspores $20–28\ \mu$. Their germination is unknown.

Infection experiments by Sawada on various species of *Colocasia* and *Alocasia* gave negative results except on forms of *C. antiquorum*. At Pusa infection experiments gave negative results on *Fagopyrum, Jasminum, Lepidium, Nicotiana, Oenothera, Opuntia, Ricinus, Salpiglossis, Schizanthus, Solanun Melongena.* and *Syringa.* A young potato plant showed a definite infection and a wounded tomato seedling gave a very indefinite infection. The only thoroughly successful inoculations were those on seedlings of *Gilia nivale.* The results are not surprising as an extention of hosts would naturally be looked for among the nearer relatives of the host, the Monocotyledons.

3. PHYTOPHTHORA ARECAE (Colem.) Pethyb.

This fungus, which was first described by Coleman (1910) as *P. omnivora Arecae,* is the cause of a very destructive disease of the Areca palm in southeastern India. It attacks the young nuts and the inflorescence covering them with a dense mycelial growth and causing the nuts to drop prematurely. Occasionally the entire tops of the trees are attacked, the hyphae even penetrating the vascular bundles.

The hyphae vary greatly in size up to 8–9 μ in diameter and bear a very few haustoria which are filiform and simple or rarely branched. More commonly there are no haustoria. The conidiophores are distinctly cymosely branched. The conidia vary considerably both in size and shape, measuring 20.6–45.4 $\times$ 30.1–71.0 μ. It appears that light is an essential factor both in the production and the germination of the conidia. The zoöspores are about 11.3 $\times$ 8 μ, with the anterior cilium measuring 20.7 μ in length and the posterior one 29 μ. The oöspores have not been observed in nature, but were produced on inoculated nuts in the laboratory. The antheridia and oögonia are described as being borne on separate branches of the same thread, the antheridium, at least in some cases, being formed first. The process of oöspore-formation is said to be similar to that described by De Bary for *P. Omnivora* and by Clinton for *P. Phaseoli.* While it is scarcely credible in the light of our present knowledge of the subject that this species really combines the processes of oöspore formation which are present in the species just mentioned, the

descriptions and figures given by Coleman indicate that this process is of the type which has been described for the two preceding species. The oöspores at maturity measure 23–38 μ in diameter.

Cross innoculation experiments were carried on with a number of plants either known to be hosts of some species of *Phytophthora,* or closely related to some known host. Zoöspores were used in each instance. Inoculations were made both with *P. Arecae* and *P. Faberi.* In addition to areca nuts and cacao pods the list included for both species of fungi members of the following genera; *Cereus, Clarkia, Oenothera, Salpiglossis, Schizanthus* and *Solanum.* "In the case of all the species experimented upon successful infection was accomplished with both fungi with the exception of *Solanum tuberosum.* It seems probable that seedlings of this plant also would be susceptible, but they were not available. In the case of *Solanum melongena* and *Lycopersicum esculentum* only seedlings proved susceptible. Inoculations of plants above 6 inches high were unsuccessful." Of three cacao pods inoculated one showed *Phytophthora* mycelium in the tissues, but did not produce conidia.

4. PHYTOPHTHORA PHASEOLI Thaxter

The first account of the oöspores of this species was given by Clinton (1906) in a paper which must rank as a classic in the literature of this genus as here are first detailed the results of the study of a species of *Phytophthora* in pure culture on agar. The oöspores occur in nature in the diseased pods and seeds of the host. They are smooth, with moderately thick walls, hyaline or light-yellowish in color, and 18–26 μ in diameter. The antheridia are hyaline, ovate to ovoid or irregular shaped bodies, which are usually applied to the base of the oögonium, and measure 8.5–11.5 $\times$ 14–17 μ. It appears that "the antheridia are not usually entirely differentiated on the thread until after contact with the oögonium." This, by the way, is quite suggestive of the description given by Blakeslee of the development of the progametes of heterothallic mucors.

In a later paper (Clinton, 1909) a more extended discussion of these phenomena is given. "In the development of the sexual

stage the antheridium is the first to appear, and is often apparently fully developed before there is much evidence of the oögonium. Whether or not the peculiar swellings spoken of earlier develop into antheridia as a result of contact with certain other threads or swellings, it is difficult to determine, but it seems most probable. This potential oögonial thread, with or without a swelling, becomes attached to the base of the antheridium and grows up along its surface toward the apex. Very often it can be seen when it has only partially covered the length of the antheridium. For a long time it was difficult to decide whether or not these threads did not actually penetrate the antheridium and grow through it, and we are not yet certain that this does not sometimes occur. Certainly the optical effect is frequently that of an internal thread with its apical walls very thin as compared with the side walls. In time, however, the oögonial thread reaches the top of the antheridium, and curving around its apex, begins to swell into the oögonium, which by this time is usually cut off from its basal thread by a septum."

To judge from the later work of Pethybridge (1913) and the illustrations from photographs which accompany the later paper by Clinton it appears that what this author really saw and described was the same type of oöspore formation as that recently described by Pethybridge and by Dastur, but that over-caution prevented him from making the proper interpretation of his observations.

5. PHYTOPHTHORA ERYTHROSEPTICA Pethyb.

The announcement by Pethybridge (1913) of this fungus is interesting as adding one more to the already long list of European diseases of the potato as well as including a second species of *Phytophthora* in the list. The fungus is doubly interesting as being the species for which was first described that peculiar method in oöspore formation which we must now consider typical of the genus *Phytophthora*.

So far as mycelial characters are concerned this species is not unlike other members of the genus. The conidia are similar to those of *P. infestans,* but larger and not so prominently papillate, although there is always a well-marked apical region with a

thicker and more transparent cell wall than is found on the remainder of the conidium. The conidia are ovate, or obpyriform due to subapical constriction, and average $20 \times 30\,\mu$. They are also very much crowded on the conidiophores which are not so highly developed as in *P. infestans,* nor are the conidia produced in such great numbers as in that species. Their germination was not noted.

The gametes are produced on separate hyphae, and at first are not well differentiated from other hyphal outgrowths. The antheridium, which is the first to appear, is a rounded or oval structure, borne laterally on the hypha from which it is soon separated by a septum. Sometimes, however, the antheridium is a true intercalary cell. In time the antheridium becomes filled with a very dense mass of granular protoplasm, apparently at the expense of the parent hypha as this becomes empty. The oögonial progamete arises in a similar manner, first appearing as a swollen knob-like body. If it comes in contact with the antheridium it grows in such a manner, as to penetrate it. The duration of this condition and the accompanying cytological phenomena have not been determined, but after a few hours, and apparently only at night, the oögonium bursts out of the antheridium and completes its development. The oögonial wall is usually thinner than that of the antheridium. As the oögonium attains its full size protoplasm ceases to migrate into it and its stalk becomes plugged, although no septum is formed. By this time the parent hypha is almost emptied of protoplasm. During the later stages of the development of the oögonium and just prior to the contraction of the protoplasm and its separation from the wall of the oögonium the contents of the antheridium begin to disappear, but in what manner was undetermined. At maturity the oösphere occupies the upper part of the oögonium, which is composed of the entire protoplasmic contents of the oösphere except small particles which adhere to the oögonial wall. The oösphere now begins to form a wall about itself, which utlimately is about $2\,\mu$ thick, smooth, and yellowish-brown in color. The mature oögonium is about $36\,\mu$ in diameter with a colorless wall which is less brittle than that of *P. infestans.* The oöspores are about $29–30\,\mu$ in diameter, or considerably smaller than those of *P.*

infestans. The method of oöspore formation in this and related species is unique among the Phycomycetes.

In nature the fungus is known only from the peculiar pink-rot of potato tubers which it produces. On solid media like oat agar, potato stalks, bread, and carrots oöspores but no conidia were produced, while the reverse was true in regard to liquid media. Conidia were produced most abundantly on a watery extract of peat soil.

6. PHYTOPHTHORA INFESTANS (Mont.) De Bary

The present species has been a storm center ever since its advent into the scientific world, while its trouble-making possibilities have not yet been exhausted. At first a battle royal waged in western Europe as to the proper name of the species which was then referred to the genus *Botrytis*. So vigorous was this warfare, and so loosely were citations given that anyone who will successfully unravel the tangle in such a way as to effectively and equitably safeguard the honors due each of the contestants, disposing of their claims in a strictly impartial and judicial manner, and arriving at a designation of the species which will meet the requirements of any recognized code of nomenclature, he will have qualified as a real "nomenclatural expert."

The next violent discussion was precipitated by the announcement by Worthington G. Smith of the discovery of the oöspores of the fungus. The results of the ensuing discussion were humorously summarized by Smith who wrote that "the oöspores became a kind of a political subject—oöspores of *P. infestans* or not oöspores of *P. infestans?*" (Clinton, 1911 b). More recently the publications of Clinton and of Jones for a time bid fair to add to the interrogation "and if oöspores, whose?"

In America two names are conspicuously associated with the investigations of the morphology of this fungus. The first note concerning what may now be regarded as probably progametes of this species appeared as an abstract (Jones & Giddings, 1909) of a paper which was not published in full. This was followed in less than a year by the announcement from the same laboratory (Jones, 1909) of the finding of oöspore-like bodies of about 30 μ diameter, but with no evidence of antheridia. These were prob-

ably chlamydospores. A little more than a year elapsed before the announcement by Clinton (1911 a) that "absolutely perfect oögonia, antheridia and even oöspores have been obtained." In the more detailed account of the discovery which appeared in a few weeks (1911 b) the various steps in the development of the oöspore are not so carefully described as were those of *P. Phaseoli,* yet the descriptions of the two species are quite similar. The illustrations which are reproduced from photographs also bear out this statement as some of them show the basal antheridium pierced by the oögonium. While no one has observed an actual fertilization to take place in species of this genius Clinton notes that in case no antheridium were present the development of the oögonium would not pass beyond the differentiation of the oösphere. This certainly precludes the suggestion that the peculiar antheridia of this and other species of *Phytophthora* are functionless. The oögonia at maturity are 34–50 μ in diameter, with a thick, reddish-brown wall. The oöspores have a medium thick wall which is smooth and hyaline. They measure 24–35 μ in diameter. The experiments which were conducted to determine the factors which govern oöspore formation do not appear to have shed any considerable light on the subject.

The final report of the investigations of Jones and his associates (Jones, Giddings & Lutman, 1912) appeared soon after these papers by Clinton. This paper is a valuable contribution to our knowledge of *P. infestans* in all its aspects. His discussion of the bodies which he terms "resting spores" differs widely from the account given by Clinton. The bodies which are described by Jones are produced in masses large enough to be barely visible to the unaided eye on account of their brown color. "Much variation in structure, grooping, and mode of development of these bodies has been observed, partly due to variations in medium. Most of these bodies have clearly been abnormal developments, or at least have failed to reach normal maturity. Indeed, we doubt if any of them are to be regarded as strictly normal. Nevertheless, it seems worth while to figure and describe the more common or striking features observed" (p. 61). Figures 1 to 20 represent various bodies found in the earlier cultures. These are borne on enlarged hyphae and enclosed in what are interpreted as ex-

cessively gelatinized walls. The solid walls of these bodies are smooth, thick, and brown. Only in a single instance was anything observed which was analogous to the formation of an oösphere. One figure (no. 15) is especially interesting as it is very suggestive of the type of antheridia which have recently been described for several species of *Phytophthora*. It may be that the majority of these bodies are chlamydospores, a structure which is known for several species of the genus.

In the later cultures a very different type of resting spores were found. These are produced, as were the others, either terminally or intercalary, have a single cell-membrane which is thickly covered with spiny tubercles. These resting spores measured 20–33 μ in diameter. The wall has two or three spots which rupture easily and suggest germ pores. The younger stages of these bodies showed 30–50 nuclei. As no bodies corresponding to antheridia were found there is no proof that these bodies are sexual spores, nor is any such claim advanced for them. The exact status of these bodies appears not to have been exactly clear to the authors as the following quotation shows. "These spores have been found in nine different strains of *Phytophthora*. These nine strains were carried continuously in culture for over three years without anything occurring to throw suspicion on their purity. . . . This fact seems to rule out the occurrence of any ordinary type of saprophyte. . . . It is not believed possible that any admixture of saprophytic growth could have entered all cultures alike, much less persist without detection. The only suggestion that seems worthy of further consideration is that these resting spores might belong to a species parasitic upon *Phytophthora* as *Piptocephalis* is upon certain moulds. De Bary, indeed, suggests such a relation as possible between *Artotrogus hydnosporus* and *Pythium debaryanum*. It would seem to us almost impossible, however, that such a condition should occur in all nine cultures alike and persist without detection during so long a period and under such varied cultural conditions" (pp. 68, 69).

These conflicting observations left the question of oöspores of *P. infestans* in a most unsatisfactory condition until the appearance of a paper by Pethybridge and Murphy (1913) which presents evidence of a nature well calculated to set the matter at rest

permanently. These authors describe and figure oöspores similar to those of *P. erythroseptica*, but considerably larger, and agreeing in all respects with those described by Clinton. As the antheridia and oögonia were found to be of the same peculiar type as those of *P. erythroseptica* the authors are led to designate Clinton's "superimposed oögonial thread" as a defective observation of the material in hand. "No spores were observed resembling in any way the resting spores with protuberances on their walls figured by Jones, and recalling *Artotrogus hydnosporus*." According to the observations of these authors when a culture once begins to form sexual organs," it continues to do so in the subsequent transfers without intermission; and although the relative abundance of these bodies may vary somewhat in the successive cultures, as a rule, the subsequent transfers from cultures rich in oögonia, become themselves in due time, also well provided with them." Several transfers covering a period of some fifteen months from the time of isolation appear to have been necessary for the formation of the oösporic habit, while about a week is necessary after making the transfer for the sexual organs to appear in the subculture. It is still an open question as to the conditions under which oöspores occur in nature, if they do so at all. A double oöspore is figured by these authors, and something approaching closely to such a condition is figured by Clinton.

Among the most interesting experiments recorded by Clinton (1911 b: 771–773) are those which concern the attempted hybridization of species. In these the first attempt was made with cultures of *P. infestans* and *P. Phaseoli*, the latter being the more vigorous species of the two and producing oöspores most abundantly. When these species were sown in the same culture "we obtained oögonia, usually only in the vicinity of the *P. infestans* colony, which were entirely different from the normal oögonia of *P. Phaseoli* that were produced abundantly all through the culture. These different *oögonia were of the P. infestans type,* which at that time we were just beginning to get in a small way in our pure cultures of *P. infestans* on oat juice agar, and they differed in that they usually *produced mature oöspores, and were far more abundant than we have ever obtained them in pure cultures of P. infestans*. . . . They also differ, perhaps, in not being so deeply

tinted, and there are some that seem to grade into *P. Phaseoli;* or at least are not very different from that species, as the oögonial walls are only slightly tinted and thickened." These hybrid oöspores were produced from the oögonia of *P. infestans* and the antheridia of *P. Phaseoli,* and measure about the same as the normal oöspores of *P. infestans.* The average measurements of *P. Phaseoli* are 22.5 μ and of *P. infestans* and the hybrids are about 30 μ. The evidence of the hybrid nature of these oöspores appears to be very strong. It would be interesting to know whether they produced fertile hybrids and if so if they are Mendelian or non Mendelian in their behavior.

Hybrids with *P. Cactorum* are also reported but are said to be much more difficult to produce. It is unfortunate that no host of this last species is given, as in the light of recent work on the genus it would be interesting indeed to know what strain of this species was used for the experiments.

Much attention is devoted by Jones to what may be called in a broad sense physiological problems, such as the relation of the fungus to its host, to culture media, to temperature, etc. Much of this data has been published previously and so need not be discussed at present except in a very general way. His observation (p. 28) concerning the production of conidia within the host is apparently the first reference to this habit in the genus *Phytophthora.* The subject of resistant varieties is discussed in considerable detail. "Well-marked and fixed differences exist among potato varieties in relative susceptibility to invasion by *Phytophthora infestans.* . . . These differences occur in foliage as well as in tuber. While foliage and tuber resistance generally go together, this relation is not invariable. The disease resistant quality is resident in large measure, and probably wholly, in the interior tissues of both leaf and tuber. In the tuber it is uniformly distributed throughout the flesh" (p. 83).

In discussing the hosts of this species reference is made to the list given by De Bary which includes "not only a number of other species of Solanaceae grown in gardens, but that he has observed it on one of the exotic species of the Scrophulariaceae, *Schizanthus grahami,* and that Berkeley has described a case where it occurred on another one of the same group, *Anthocercis*

viscosa, from New Holland." At the risk of appearing to be trite we may remark in passing that not only has there been advances made in mycology, but in other fields of botany as well in the past third of a century. Moreover some geographic names have also changed. New Holland is one of these, being labeled on our maps to-day New Guinea. As to the hosts in question both genera appear among the Scrophulariaceae in De Candole's Prodromus while in Engler and Prantl's Pflanzenfamilien they both appear under Solanaceae. In other words De Bary's taxonomy and geography were correct in his own day. This same reference to scrophulariaceous hosts is quoted by Lindau[2] and is given by Clinton as a reason for suspecting the validity of *P. Thalictri.*

Various theories have been advanced as to the means by which the present species maintains itself from year to year, one of them being that the fungus lives over in the soil or in the diseased tubers and débris from the crop. A paper by Stewart (1913) details some experiments on this question. Soil was taken from a field which had produced a crop of blighted potatoes. Diseased and partially decayed tubers and blighted stems were placed in the soil which was subsequently kept outdoors until spring, when it was planted with tubers procured from a blight-free field and treated with disinfectants. No infection occurred, nor could it be induced by painting the leaves with mud prepared from this soil and the diseased potatoes. The author considers his results inconclusive, but indicating that it is highly improbable that the disease persists in the soil over winter.

7. PHYTOPHTHORA THALICTRI Wilson & Davis

The oöspores of this species were found by Clinton (1909: 894) who says that "so far as could be determined, the antheridia and oögonia were developed from different mycelial threads." In the light of present knowledge this would indicate that these organs are of the same nature as those of *P. infestans.* The oögonia are reddish-brown, a little deeper tinted than those of *P. Phaseoli,* moderately thin walled, and measuring 25–33 μ in diameter. The oöspores are hyaline or very light colored, with medium thick,

[2] Sorauer. Pflanzenhr. ed III. 2: 140. 1908.

smooth wall, and measuring 18.5–25 μ in diameter. "Those seen by the writer," says Clinton, "did not differ materially from the oöspores of *P. Phaseoli*, so that we may expect those of *P. infestans*, when found, to be of similar character."

The fungus was not obtained in pure culture. Inoculations were made direct from the diseased leaves to the cut surface of potatoes and onto young tomato plants in the greenhouse. All failed, as did the attempts to produce the fungus on *Thalictrum* by inoculating it with a pure culture of *P. infestans*, which at the same time was able to infect potatoes. Concerning the identity of the present species and the results of his inoculations Clinton says, "since *P. Thalictri* resembles *P. infestans* so closely, the writer has thought that possibly they might not be distinct species. Worthington G. Smith (Diseases of Field and Garden Crops, pp. 275–6) gives a list of different hosts of *P. infestans* which include even two Scrophulariaceae. . . . While these experiments were probably not extended enough to speak positively, still they at least indicate that these fungi are distinct strains, if not distinct species" (p. 895). Personally the present writer regards these experiments as far more conclusive evidence of the distinctness of the two species in question than would the success of any of these inoculations have been of the identity of these fungi. The question which is raised concerning the hosts of *P. infestans* has been noted under that species.

The statement made by Clinton concerning the identity of *P. Thalictri* is misquoted by Dastur (p. 225) who speaks of "*P. Thalictri*, which Clinton suspects to be identical with *P. Phaseoli*.

8. PHYTOPHTHORA FAGI (Hartig) Hartig

This fungus attacks the beech seedlings in Europe, often proving quite destructive. It first attacks the cotyledons, then spreads to other parts of the plant. A large number of other tree and herb seedlings are known to be subject to the attacks of a *Phytophthora* in Europe and it is not improbable that there is but a single species of the genus concerned in seedling diseases. This, however, has not been investigated in recent years. We are indebted to Himmelbaur for a careful comparative study of this

species and the demonstration of its validity. The results of these studies are discussed under *P. Cactorum.*

9. PHYTOPHTHORA CACTORUM (Lebert & Cohn) Schröt.

This species was originally described from diseased cacti in Europe and was later included along with other forms by De Bary in his *Phytophthora omnivora.*

Comparative studies were made by Himmelbaur (1911) on three forms which might well be included in De Bary's species. They were designated *P. Cactorum, P. Fagi,* and *P. Syringae.* The cultures of *P. Cactorum* were obtained from *Phyllocactus* at Dahlem. As a result of his inoculation experiments with these fungi on three species of cacti he concludes that inoculation experiments are of very little value in delimiting species. However the results of his inoculations, which he presents in tabulated form, are quite interesting so they are quoted in their entirity.

Host	Macroscopic			Microscopic		
	Cactorum	Fagi	Syringae	Cactorum	Fagi	Syringae
Echinopsis Eyriesii	Much affected	Much affected	± Slight infection	Very numerous oöspores	Very numerous oöspores	Numerous oöspores
Cereus tephracanthus	± Slight infection	± Slight infection	Slight infection	Numerous oöspores	Numerous oöspores	Few oöspores
Cereus Martianus	± Slight infection	Slight infection	± Slight infection	Numerous oöspores	Few oöspores	Numerous oöspores

All three forms were grown in Erlenmeyer flasks on sterilized carrots and in Petri dishes on various media. *P. Cactorum* made the most vigorous growth while *P. Syringae* was the weakest. He considers these forms all closely related but morphologically distinguishable both by conidial and oösporic characters as well as by the mycelium. He also expresses the opinion that *Peronospora Sempervivi* Schenk is identical with *Phytophthora Cactorum.* The results of his morphological studies are given in tabular form for ready comparison.

	P. Syringae	*P. Fagi*	*P. Cactorum*
Mycelium:			
	Hyphae slender, regular, intercellular, in culture submerged, apically monopodially much branched.	Slender, regular, intercellular or intracellular, in culture both aerial and submerged, apically scantily monopodially branched.	Very irregular in form, in culture both aerial and submerged, somewhat irregularly branched.
	Haustoria simple or ganglionate and digately branched, cylindric.	Simple or branched, cylindric, or apically enlarged irregularly.	None.
	Conidiophores sympodially branched and thickened below the conidia.	Sympodially much branched and thickened below the conidia.	Not typical sympodial in branching, conidia often borne in clusters.
	Conidia elongate ovate, papillate, apex thick walled, produced tardily, size 40–74 × 30–32 μ.	More or less regularly ovate, papillate, produced abundantly, size 30–40 × 15–30 μ.	Roundish to ovate, very noticeably papillate, very variable in shape and size.
Oöspores:			
	Oögonia globoid, intercallary, seen only in water cultures.	Pyriform, rounded at base, intercallary, seen in water and agar cultures.	Globoid, apical, seen in both water and agar cultures.
	Antheridia borne near the oögonium, tube not seen, relation to oögonium indefinite.	Borne near the oögonium, tube present, applied basally.	Borne near the oögonium, rarely seen in water cultures, applied laterally.
	Oöspore with medium thick, smooth, yellow wall, size 30 μ.	With medium thick, smooth, yellow wall, size 20–30 μ.	With medium thick, smooth, brown wall, size 30–45 μ.

As a result of this comparative study it is very evident that these three forms are distinct species. The next question to present itself is that of the identity of the form which De Bary studied and named *P. omnivora*. From the evidence presented by De Bary in his paper Himmelbaur is inclined to the belief that the form was at least similar to *P. Fagi*, if not identical with it.

In old agar cultures which had begun to degenerate forms appear which are suggestive of *Vaucheria*, from which the author concludes that the genus *Phytophthora* may represent a degenerate state of *Vaucheria*.

The phenomenon of zonation in cultures was studied and the conclusion reached that it is due to variation in temperature.

10. PHYTOPHTHORA SYRINGAE (Klebh.) Klebh.

This fungus has been studied by three investigators who agree as to its morphology. Klebahn (1909) published a comprehen-

sive study of the fungus, including many inoculation experiments to determine its possible host limitations. He was able to secure an abundant infection with the production of oöspores on *Syringa persica, Lygustrum vulgare, Jasminum nudiflorum, Forsythia viridissima* and *Crataegus oxycantha,* while the twigs were killed on *Pirus communis* and *Prunus cerasus* without the formation of oöspores. Indifferent infection was obtained on species of *Acer, Aesculus, Alnus, Corylus, Quercus, Tilia, Pirus, Malus* and *Prunus domestica.* Complete failure was recorded for *Azalia, Betula, Carpinus, Fagus, Fraxinus, Juglans, Philadelphus, Plantanus, Salix, Sorbus, Erica* and *Calluna.* While the infection of the pear would at first sight indicate a possibility of the identity of *P. Syringae* with the species reported on pomaceous fruits, but the failure to infect the apple makes the probability of the identity of the two entirely out of the question.

The morphological characters of the species are included in the summary of the work of Himmelbaur under *P. Cactorum.* The fungus has recently been found in Holland, where it was carefully studied, especially from the standpoint of its economic importance, by Schoevers (1913), whose observations on the morphology of the fungus and its effect upon its host are in accord with the preceding papers. The statement is made that the conidia are unknown in nature. It is, therefore, interesting to note that almost thirty years earlier than any of these papers Berkeley (1881) described a fungus from the leaves of the lilac in Scotland which caused a blackening of the host similar to that caused by *P. infestans* on the foliage of the potato. The opinion was expressed that the two fungi were very closely related, although the lilac inhabiting species was christened *Ovularia Syringae.* In a subsequent paper Smith (1883) described bodies which he termed resting spores from decaying leaves, but his notes are insufficient to indicate the exact nature of the bodies which he found. A third note by the discoverer of the fungus (Wilson, 1886) describes in a somewhat fantastic manner the germination of the conidia by the formation of zoöspores. The fungus appears in Saccardo under Berkeley's name while the only figure cited is that which accompanied the original description. Apparently Saccardo saw nothing in this later sketch to indicate

that the species in question has other relationships than those indicated by its name. Indeed it is a true *Phytophthora* and apparently identical with *P. Syringae.*

The complete synonomy of the fungus then becomes, *Ovularia Syringae* Berk. (1881), *Phleophythora Syringae* Klebh. (1905), *Phytophthora Syringae* (Klebh.) Klebh. (1909). Here is a nomenclatural tangle which is not strictly amenable to the rule of priority. The oldest name of the species is that given it by Berkeley, yet if *Ovularia Syringae* were to be transferred to *Phytophthora* the combination would be untenable as there is already an older *Phytophthora Syringae,* which is based on *Phleophythora Syringae,* a name which is untenable because it is antedated in the synonomy of the species. Perhaps this case comes under the "nomina conservenda" and so will not need to be renamed, but be allowed to carry the specific name which Klebahn gave it.

11. PHYTOPHTHORA NICOTIANAE Van Breda de Haan

Our information concerning this species is derived from the monographic treatment of the species by its author. It is a member of the cactorum group of species, *i. e.,* its antheridium is of the normal type for the Oömycetes. So far it has been recorded only from the East Indies.

13. PHYTOPHTHORA FABERI Maub.

The literature of this species is quite extensive, yet there are a number of points concerning its life history which are far from clear. In the earlier papers the species is referred to as *P. omnivora* De Bary. Perhaps the first careful morphological study of the fungus was that of von Faber (1910) who obtained his material from Kamerun on cacao pods. He considers the fungus distinct from *P. omnivora,* but quite similar to that species. He describes the mycelium as being provided with haustoria and being both intercellular and intracellular, in extreme cases penetrating the seeds, but usually confined to the pods. The conidiophores are 150–200 μ high, bearing one or two conidia, which average $25 \times 30\,\mu$ or rarely as large as $42 \times 80\,\mu$. The

zoöspores are very numerous, as many as twenty issuing from a single conidium. The oöspores were found in abundance, throughout the infected tissue, but no trace of either antheridia or oögonia. As subsequent investigators have also failed to find the gametes it is now usually conceded that these bodies are in reality chlamydospores. The fungus is considered by von Faber to be coextensive in distribution with the cacao, although epidemic outbreaks have been confined to the American tropics, to Ceylon, and to Kamerun. Apparently drawing on von Faber's account of the fungus for his data Maublanc named it *P. Faberi.*

Infection experiments were first reported by Rorer (1910 a, b) who proved that the pod-rot and the canker of cacao are both caused by the same fungus. He gives a detailed study of the pathology of the organism, concluding that the trunks become infected by the migration of the mycelium from the pods through the twigs. This work was confirmed in Ceylon by Petch (1910) who extended his experiments to the fruit-rot and canker of *Hevea.* He demonstrated the identity of these diseases. "On plantations of *Hevea* only 'canker' has not caused very much damage, but on mixed *Hevea* and cacao plantations it is decidedly more serious." The fungus evidently spreads from the one host to the other in the field.

The correctness of the results obtained by Rorer has been questioned by Essed (1912) who was unable to duplicate the work. He suggests that the trees used might have already been infected with the true cause of the canker, which he considers to be some species of *Lasidiplodia, Nectria* or *Spicaria,* or some other related form. He asks "Why should Mr. Rorer obtain results different from mine? Was it due to the difference between his mode of operation and mine? To be sure, he operated with full grown trees and I did so with seedlings; his trees were standing in the open field and my seedlings were raised and kept under rigorously sterile conditions." The statement of the case by Essed may contain the answer to his inquiry. It is well known that certain fungi attacking mature hosts will not attack the juvenile stage of the same host plant. The reverse is also true. Moreover the "rigorously sterile conditions" under which these experiments were made might have been so thorough that *Phytophthora* could not grow.

Further studies of the species were made by Coleman (1910), who found that in water cultures the conidiophores often bore as many as twenty conidia. Chlamydospores were produced in his cultures in abundance, but oöspores were absent. Extensive infection experiments were carried on in connection with those on *P. Arecae,* under which species they are detailed. In addition the cacao fungus was inoculated onto Areca nuts, obtaining a slight infection in one instance. He named the fungus *P. Theobromae* giving as its hosts, on the authority of Petch, *Theobroma Cacao, Hevea brasiliensis* and *Artocarpus incisa.* In a postscript to his article he notes that "since the above was written an article by Petch . . . has brought to my attention the fact that the cacao fungus has been already given the name of *Phytophthora Faberi.*" In listing the species of the genus Pethybridge includes *P. Faberi* which is "possibly synonymous with *P. Theobromae.*"

From the fact that this fungus is more destructive in the American tropics than elsewhere it is not impossible that this is its home. This is further borne out by the fact that in the West Indies it attacks a second species of *Theobroma,* while its two chief hosts are American in origin. Indeed the bread-fruit is the only well authenticated host of oriental origin, and on this its occurrence appears to be quite limited.

13. PHYTOPHTHORA OMNIVORA De Bary

All members of the genus *Phytophthora* which were not referable to *P. infestans* were collected together under this name by De Bary. So constituted the species included all those forms of the genus found on seedlings and succulents in Europe. Recent work has shown some of these forms to be morphologically distinct, so that it is now a question as to just how much, if any, of the original mass of material can remain under this name.

Since the time of De Bary various writers have added their mite to increase the confusion until to-day the species as usually recognized is indeed a "waste basket" into which is thrown any unidentified *Phytophthora.* Some of these have recently been removed and given their proper status as species, while others which have been adequately studied by their discoverers have

escaped a fate which might have been theirs had they fallen into other hands. The existing confusion lead Coleman (p. 620) to say that "it would appear that a careful revision of the species *Phytophthora omnivora* is needed and this seems particularly necessary for those fungi from outside of Europe which have been identified as this species." It is, however, today the European forms of the species which are in most need of a careful revision.

From time to time a rot of pome fruits has been noted from Europe and ascribed to this species. It was first reported by Osterwalder (1906) on apples in Switzerland. As inoculations on *Sempervivium tectorum* were successful it was referred to this species. A rot of pears in Belgium was recorded by Marchal (1908) and in Bohemia by Bubák (1910), both of whom also refer the fungus to the present species. More recently Osterwalder (1912 *a*) has added the strawberry to the list of fruits attacked, recording a serious outbreak in Switzerland. The same author (Osterwalder, 1912 *b*) records an attack upon young apple nursery stock in which some varieties had almost all the twigs killed. As these young trees grew adjoining the strawberry patch which was so seriously infected it was presumed that this was the source of infection. In all these cases both conidia and oöspores were produced in abundance. The figures and descriptions indicate that more than one species of *Phytophthora* may be concerned and that in all probability none of these outbreaks were really due to the species which is credited with the damage.

Another European record under the name of this species is also furnished by Osterwalder (1909) who found a *Phytophthora* attacking *Calceolaria*. To judge both by the host and the description this may be referable to *P. Cactorum* as now understood, but further information concerning the fungus on this host is highly desirable.

The nutmeg tree (*Myristica fragrans*) in Java suffers from attacks on its leaves and growing twigs by a fungus which Zimmermann (1907) has identified as "*Phytophthora* spec. (*Ph. omnivora* de Bary?)." The conidia are ovate, prominently papillate, with a portion of the conidiophore adhering as a pedicel, measuring 20–60 $\times$ 17–30 μ. The conidiophores are typical of the

genus. No oöspores were found. The pedicel adhering to the conidia suggests a relationship with *P. Colocasiae,* although it is a distinct species, and apparently quite dissimilar to the average run of the oriental species of the genus.

The latest addition to the list of pests referred to this species was first reported by Hori (1907) as attacking ginseng in Japan and in Ohio. Since that time it has been found to be a widespread pest in ginseng beds in the United States. This fungus is certainly incorrectly identified. It is described as having simple conidiophores measuring $95 \times 7\,\mu$ and emerging from the stomata. The conidio are elliptic to ovate, $30–50 \times 50–60\,\mu$, prominently papillate, and having a very short basal pedicel. The oöspores are thick walled, light brown in color, and measuring $26–28\,\mu$.

SPECIES INQUIRENDAE

Three additional members of the genus have found their way into literature, yet are of doubtful standing on account of their improper introduction. Mention is made by Gandara (1909) of a *P. Agaves* Villada on the mayguey in Mexico, but no description or figure is given of the fungus. *P. Jathropiae* Petersen has been distributed by the "Centralstelle für Pilzkulturen" but is as yet undescribed. An unnamed species of *Phytophthora* is mentioned by Möller (1901) as occuring on the "figs imported from Europe to Brazil" and at least locally causing considerable damage in gardens. The liminiform conidia are prominently papillate and measure $38–45 \times 100–200\,\mu$. The conidiophores are $100–200\,\mu$ high. The relationship of the fungus is quite obscure as the only species of the genus with which he appears to have been acquainted is *P. infestans.* The fungus may be an European export, in which case it is probably closely related to the other fruit-rotting forms.

CROSS INOCULATIONS

One of the most interesting results of the work on species of *Phytophthora* in the last four or five years is the peculiar and altogether unexpected outcome of the numerous cross-inoculation experiments. A comparison of the results published by the vari-

ous authors tends to throw decided doubt upon the value of this method of delimiting species in this genus, as practically any species of Spermatophyta which is in nature subject to the attacks of any *Phytophthora* is likely under laboratory conditions to be more or less severely attacked by almost any other species. Indeed some of the hosts recorded for various species of the genus are not known to harbor these fungi in nature. It would appear, then, that the parasitism of *Phytophthora* is of such a low order that it will not admit of their being differentiated into races as are certain of the Uredineae for example.

CULTURE MEDIA

Such a discussion as the present would scarcely be complete without a brief mention of the methods and media employed in the pure culture work discussed above. Some of these media are very simple in their nature, but often serving an important purpose in the life history studies on these fungi. Such media are vegetable plugs of various kinds, decoctions of fruits and even of peaty soil, and in the case of one investigator flies were used in distilled water.

The best success has been obtained from growing these fungi on agar made with grain or leguminous seeds as its chief food base. Of these peas, beans and oats have proven most efficient and satisfactory. Such culture media may be made by the following formula, the various seeds and grains remaining constant. Ground beans 40 grams, agar 15 grams, water 1 liter. Prepare in double boiler, or in the autoclave, filtering through absorbent cotton. In case of oats it is preferable to boil 100 grams of ground oats in a liter of water using a double boiler and cooking the oats for two or three hours. Strain and add the other ingredients and sterilize. Species of *Phytophthora* prefer a slightly acid medium (+ 5 to + 10 Fuller's scale).

Synthetic media have received considerable attention from a number of investigators as such media would give a basis of accurate physiological observations. So far this does not appear to have been over successful. The rather extensive series of experiments conducted by him have led Jones to conclude that

low osmotic pressure is necessary to the proper development of *P. infestans* and that it is "limited to certain combinations of chemicals as sources of carbon, nitrogen, and energy. The only really efficient single carrier of these which was found is asparagin, and the availability of this substance seems to be dependent upon the presence of other chemicals" (pp. 51, 52). His most successful formula is as follows: Potassium phosphate 0.25 gm., potassium chlorid 0.05 gm., potassium nitrate 0.5 gm., magnesium sulphate 0.1 gm., calcium carbonate 0.025 gm., asparagin 0.5 gm., water 1 liter.

In the course of his extensive studies on the germination of the conidia of *P. infestans* in relation to various substrata Garbowski (1913) devoted considerable attention to the subject of synthetic media with the result that he recommends Knop's solution with the addition of glucose (0.2 gm. to 50 c.c.).

TAXONOMIC CONSIDERATIONS

From the discussion of the various species of the genus it is evident that there are two distinct types of sexual organs present in species which have been referred to *Phytophthora*. When De Bary described the oöspore formation in *P. omnivora* his account showed nothing which did not agree with the process as we know it in *Peronospora*. Recent investigations have confirmed this on *P. Fagi, P. Cactorum,* and *P. Syringae,* while the description of *P. Nicotianae* indicates that it belongs to the same group of species. These species have been designated by Pethybridge as the *Cactorum-group*. In *P. Faberi* the sexual reproduction is unknown, while in the remaining species of the genus the sexual organs are of the peculiar type described by Pethybridge and by Dastur. The group of species producing this type of gametes has been called in like manner the *infestans-group*. Here we find a mode of sexual reproduction which is unique among the Phycomycetes. So distinct is this method of oöspore formation that Pethybridge proposes to separate the species which possess it into a new family, calling it *Phytophthoraceae*. While the remaining species are retained in the family *Peronosporaceae* under the generic name *Nozemia*. While the process of oögenesis is so poorly understood at present, yet it is apparent from the peculiar

type of gametes and the complete absence of periplasm in the oögonium that the family *Phytophthoraceae* may perhaps be considered as constituting the order *Phytophthorales.*

The name *Nozemia* for the *Cactorum-group* of species is entirely unnecessary, as one of the species included in this new genus is itself the type of a monotypic genus. When Klebahn first published an account of *P. Syringae* he had only the oöspores which he recognized as belonging to the *Peronosporales*, and in absence of conidia he described the fungus as *Phleophythora Syringae.* As the genus was founded on the sexual phase of a polymorphic fungus certainly there can be no objection to its validity forthcoming from an adherent of the European views on the nomenclature of such fungi. Klebahn's name must, therefore, take the precedence, with the following species: 1. **Phleophythora Syringae** Klebh. (*Phytophthora Syringae* Klebh.), 2. **P. Fagi** (Hartig) n. nom. (*Phytophthora Fagi* Hartig), 3. **P. Cactorum** (Lebert & Cohn) n. nom. (*Peronospora Cactorum* Lebert & Cohn, *Phytophthora Cactorum* Schröter), 4. **P. Nicotianae** (Van Breda de Haan) n. nom. (*Phytophthora Nicotianae* Van Breda de Haan).

P. Faberi on account of its imperfectly known life history cannot be definitely assigned to a genus, so it may well remain as at present placed. As *P. omnivora* is here recognized as an aggregate of undetermined affinity it need be considered no further.

NEW BRUNSWICK,
NEW JERSEY.

BIBLIOGRAPHY

Berkeley, M. J.

1881. Lilac fungus.—Gard. Chron. II. 16: 665. *f. 135.*

Bubák, F.

1910. Die Phytophthorafäule der Birnen im Böhmen.—Zeitschr. Pflanzenkr. 20: 256–261. *pl. 4 + f. 1, 2.*

Butler, E. J. & Kulkarni, G. S.

1913. Colocasia blight caused by *Phytophthora Colocasiae* Rac.—Bot. Mem. Dept. Agr. India 5: 233–261. *pl. 1–4.*

Clinton, G. P.

1906. Downey mildew, *Phytophthora Phaseoli* Thaxt., of lima bean.—Rept. Connecticut Agr. Expt. Sta. **1905**: 278–303. *pl. 20–22.*

Clinton, G. P.

1909. Artificial cultures of *Phytophthora,* with special reference to oöspores. —Rept. Connecticut Agr. Expt. Sta. **1907–08**: 891–907. *pl. 71–75.*

1911 *a.* Oöspores of potato blight.—Science, n. s., **33**: 744–747.

1911 *b.* Oöspores of the potato blight, *Phytophthora infestans.*—Rept. Connecticut Agr. Expt. Sta. **1909–10**: 753–774. *pl. 38–40.*

Coleman, L. C.

1910. Diseases of the areca palm (*Areca Catechu* L.) I.—Koleroga or rot disease.—Ann. Myc. **8**: 591–626. *pl. 7–9 + f. 1–3.*

Coleman, L. C.

(Note.—This paper was reissued with new pagination and with additional illustrations as Myc. Bull. Dept. Agr. Mysore **2**: 1–92. *pl. 1–81 + f. 1–6.* 1910.)

Dastur, J. F.

1913. On *Phytopthtora parasitica* nov. spec. a new disease of the castor oil plant.—Bot. Mem. Dept. Agr. India **5**: 177–231. *pl. 1–10.*

Essed, E.

1912. Cacao canker.—West Indian Bull. **12**: 302–308.

Faber, F. C. von.

1909. Die Krankheiten und Parasiten des Kakaobaumes.—Arbeit. Kais. Biolog. Anstalt Land- u. Forstw. **7**: 193–351. *pl. 2, 3 + f. 1–51.*

Gandara, G.

1909. Nota acerca de los enfermadodes fungosas del maguey.—Mem. y Rev. Soc. Cient. Antonio Alzate **25**: 293–305.

Garbowski, L.

1913. Keimungsversuche mit Konidien von *Phytophthora infestans* de Bary. —Cent. Bakt. II. **36**: 500–508. *pl.*

Hecke, L.

1898. Untersuchungen über *Phytophthora infestans* De Bary, als Ursache der Kartoffelkrankheit.—Jour. f. Landw. **46**: 71–74. *pl. 1, 2.*

Himmelbaur, W.

1911. Zur Kenntnis der Phytophthoreen.—Mitth. Botan. Staatsinst. Hamburg **1910**: 39–61. *pl. + f. 1–14.*

Hori, S.

1907. A disease of Japanese ginseng caused by *Phytophthora Cactorum.*— Bull. Imp. Cent. Agr. Expt. Sta. Japan 1^2: 152–162. *pl. 27.*

Jones, L. R.

1909. Resting spores of the potato fungus (*Phytophthora infestans*) — Science, n. s., **30**: 813, 814.

Jones, L. R. & Giddings, N. J.

1909. Studies of the potato fungus, *Phytophthora infestans.*—Science, n. s., **29**: 271. (Abstract.)

Jones, L. R., Giddings, N. J. & Lutman, B. F.

1912. Investigations of the potato fungus, *Phytophthora infestans.*—U. S. Dept. Agric. Plant Indust. Bull. **245**: 3–100. *pl. 1–10 + f. 1–10.*

(Note—This paper was reprinted from the same plates in 1913 and reissued as Bull. Vermont Agr. Expt. Sta. 168. The two editions are in every way identical except that the colored plates are omitted from the Vermont edition.)

Klebahn, H.

1909. Krankheiten des Flieders, pp. 75. *f. 45.* Berlin.

Marchal, E.

1909. Sur une maladie nouvelle du poirier.—Bull. Soc. Roy. Bot. Belgique **45**: 343, 344.

Möller, A.

1901. Phycomyceten und Ascomyceten, in A. F. W. Schimper, Botanische Mittheilungen aus den Tropen. Pp. xii, 319. *pl. 11.* Jena.

Osterwalder, A.

1906. Die Phytophthorafäule beim Kernobst.—Cent. Bakt. II. **15**: 435–440.

1909. Unbekannte Krankheiten an Kulturpflanzen und deren Ursache.—Cent. Bakt. II. **25**: *260–270. pl. 1, 2.*

1912 *a.* Die Phytophthora-fäule die Erdbeeren.—Landwirt. Jahrb. Schweiz. **19**: 320, 321.

1912 *b.* Das Absterben von Veredlungen, versucht durch *Phytophthora.*—Landw. Jahrb. Schweiz. **19**: 321, 322.

Petch, T.

1910. Cacao and Hevea canker.—Cirs. and Agr. Jour. Royal Bot. Gard. Ceylon **5**: 143–180.

Pethybridge, G. H.

1913. On the rotting of potato tubers by a new species of *Phytophthora* having a method of sexual reproduction hitherto undescribed.—Sci. Proc. Royal Dublin Soc., n. s., **23**: 529–565. *pl. 42–44.*

Pethybridge, G. H., & Murphy, P. A.

1913. On pure cultures of *Phytophthora infestans* De Bary, and the development of oöspores.—Sci. Proc. Royal Dublin Soc., n. s. **13**: 566–588. *pl. 45, 46.*

Rorer, J. B.

1910 *a.* The relation of black rot of cacao pods to the canker of cacao trees.—Bull. Trinidad Dept. Agric. **9**: 38.

1910 *b.* Pod rot, canker, and chupon wilt of cacao caused by *Phytophthora* sp.—Bull. Trinidad Dept. Agric. **9**: 79–103. *pl. 9–17.*
(Note—The reprint of this article is paged 1–24.)

Sawada, K.

1911. Infection of the taro.—Reprinted from Special Reports of the Formosa Agr. Expt. Sta. (Japanese—quoted by Butler and Kulkarni.)

Schoevers, T. A. C.

1913. Eene voor Nederland nieuwe Seringenziekte, veroorzaakt door *Phytophthora Syringe* Klebahn.—Tijd. Plantenz. **19**: 41–64. *pl. 1, 2.*

Smith, W. G.

1883. Resting spores of the llilac fungus.—Gard. Chron. II. **20**: 439.

Stewart, F. C.

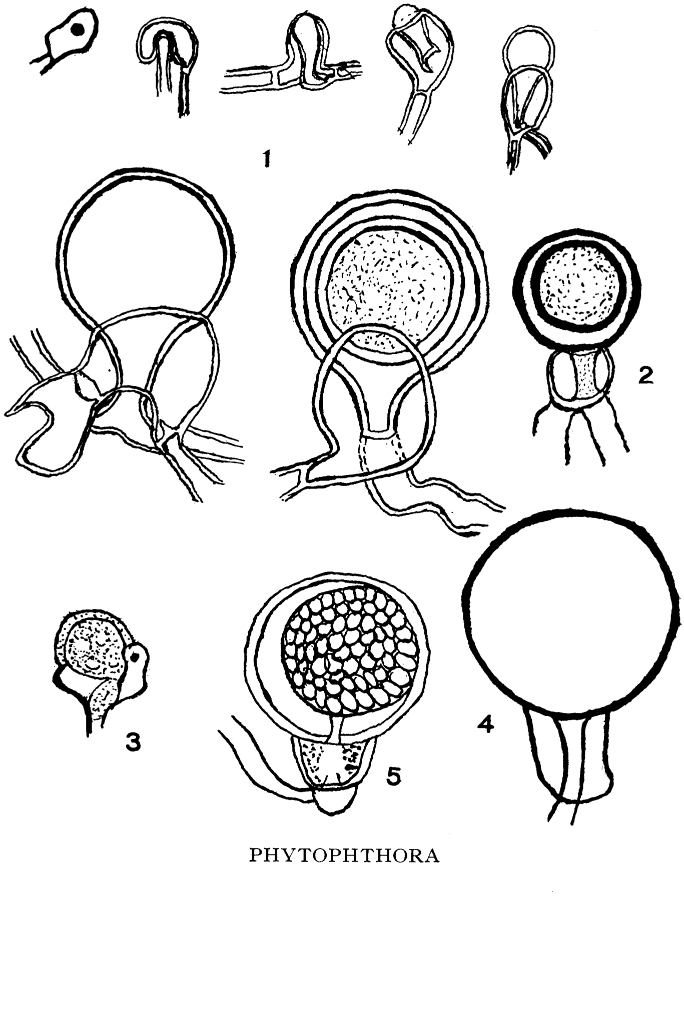
1913. The persistence of the potato late-blight in the soil.—Bull. New York State Agr. Expt. Sta. **367**: 357–361.

Wilson, A. S.

1886. Birth of an Ovularian zoöspore.—Gard. Chron. II. **26**: 815. *f. 159.*

Zimmermann, A.

1907. Ueber einige an tropischen Kulturpflanzen beobachtete Pilze—I.—Cent. Bakt. II. **7**: 101–106, 138–147. *f. 1–24.*



PHYTOPHTHORA

EXPLANATION OF PLATE CXIX

Fig. 1 *Phytophthora parasitica.* Seven stages in oôgenesis. After Dastur.

Fig. 2. *Phytophthora Phaseoli.* Oöspore. After photograph by Clinton.

Fig. 3. *Phytophthora infestans.* Resting spore. After Jones, Giddings, and Lutman.

Fig. 4. *Phytophthora infestans.* Oöspore. After photograph by Clinton.

Fig. 5. *Phytophthora Arecae.* Oöspore. After Coleman.